

Comparative Diets and Growth of Two Scombrid Larvae, Chub Mackerel *Scomber japonicus* and Japanese Spanish Mackerel *Scomberomorus niphonius*, in the Central Seto Inland Sea, Japan

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Abstract

Occurrence, distribution, feeding habits and growth during the early life stages of two scombrids, chub mackerel *Scomber japonicus* and Japanese Spanish mackerel *Scomberomorus niphonius*, were studied to elucidate their early life histories. Larvae and early juveniles were collected by larva-net tows and commercial boat seine fisheries in the central Seto Inland Sea, Japan in 1995 and 1996. Larvae of the two mackerels were caught in both May and June, with peak abundance in late May for chub mackerel and in early June for Japanese Spanish mackerel. Analysis of gut contents revealed that the feeding habits of chub mackerel larvae were complex compared to those of Japanese Spanish mackerel larvae. Most of the gut contents of chub mackerel larvae were composed of Copepoda, Appendicularia and other invertebrate plankters. Fish larvae were found in the guts of chub mackerel larvae larger than 5 mm SL and its occurrence rate increased as growth proceeded. On the other hand, Japanese Spanish mackerel larvae fed almost exclusively on fish larvae from the first feeding. The growth rate during larval and early juvenile stages of Japanese Spanish mackerel (1.47 mm/day), assessed by otolith microstructure, was higher than that of chub mackerel (0.71 mm/day). Japanese Spanish mackerel larvae could be considered to have a unique food habit which results in extremely rapid growth and reduced vulnerability to predation in the early life stages.

Two scombrid fishes, chub mackerel *Scomber japonicus* and Japanese Spanish mackerel *Scomberomorus niphonius*, are commonly found along the coastal waters of Japan. Spawning migration of the two species from oceanic waters (the northwestern Pacific) into the Seto Inland Sea (Fig. 1) occurs during the spring (Mito, 1965; Kishida and Aida, 1989). Although chub mackerel is an important fisheries resource, there is no information on its survival or recruitment in the Seto

Inland Sea. Comprehensive biological studies on the early life history of chub mackerel were conducted mainly in the oceanic waters around Japan, such as the Kuroshio and the Tsushima Current regions (Watanabe, 1970; Uchida *et al.*, 1958). Feeding habits of larval chub mackerel were investigated in the southeastern Pacific (Lipskaya, 1982) and southeastern waters of Japan (Yokota *et al.*, 1961). Japanese Spanish mackerel is one of the most important fisheries resources in the Seto Inland Sea, where total catch exceeded 6,000 t in the mid 1980s. The stock biomass, however, has been decreasing and is less than one-twentieth of that in the 1980s. In the central Seto Inland Sea, one of the main spawning grounds of Japanese Spanish mackerel, the total catch has decreased to 74 t in 1997, while that of chub mackerel has increased to ca. 500 t in the 1990s (Fig. 2).

In order to stabilize the catch and to establish more effective fisheries management, it is necessary to understand the early life histories and recruitment processes of these species. Here, we describe the early life histories of chub mackerel and Japanese Spanish mackerel in the Seto Inland Sea with emphasis on larval piscivory.

Methods and Materials Three sampling regimes were carried out in the Hiuchi-nada, central waters of the Seto Inland Sea, Japan (Fig. 1). One set of surveys was conducted on the larval occurrence of chub mackerel and Japanese Spanish mackerel (cruise SO) two to three times per month, from March to June 1995 and April to June 1996, on the RV Hiuchi (4.9 t) and RV Yuri (4.9 t) of Ehime Prefecture Chuyo Fisheries Experimental Station. Ten-minute middle layer tows with a conical larva-net (mouth diameter 1.3 m, mesh aperture 1.0 mm) were made to collect these species.

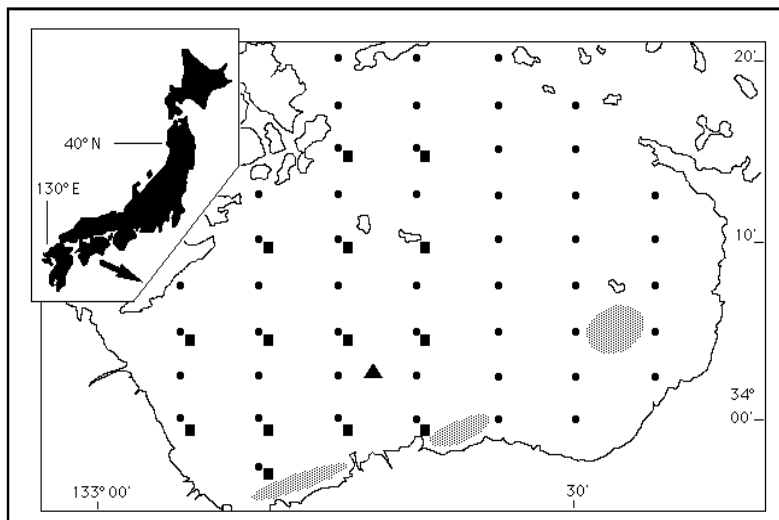


Figure 1. Map of the Hiuchi-nada, central waters of the Seto Inland Sea, showing the sampling area where ichthyoplankton was collected in 1995 and 1996. Closed squares indicate stations sampled for seasonal occurrence and closed circles stations sampled for distribution of chub and Japanese Spanish mackerel larvae, respectively. Shaded areas indicate areas where the boat seine fishery operated.

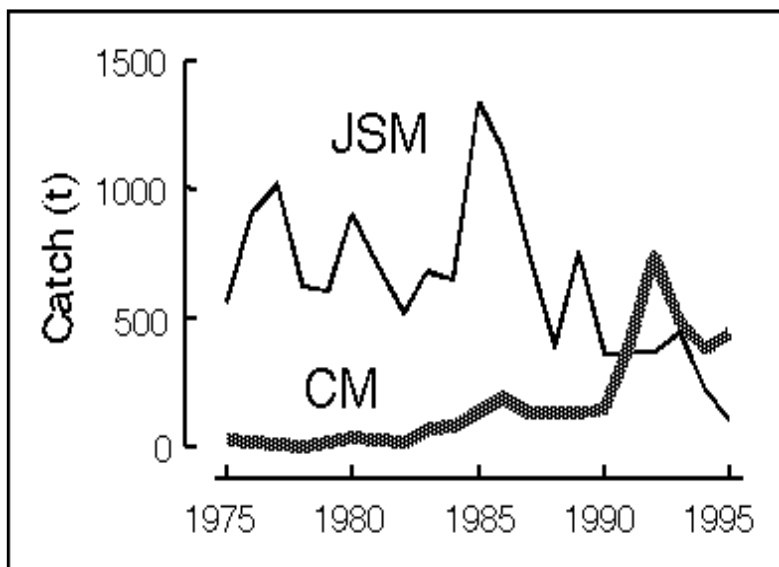


Figure 2. Trends of annual catch of chub mackerel (CM) and Japanese Spanish mackerel (JSM) in the Hiuchi-nada, central waters of the Seto Inland Sea, 1975 to 1995.

Another set of surveys was performed to study the horizontal distribution of mackerel larvae (cruise SH) during cruises of the RV Shirauji-maru (138 t) of National Research Institute of Fisheries and Environment of the Inland Sea on 27-30 May and 18-21 June 1996. Oblique hauls were made from the surface to 5 m above the sea floor using a bongo net (mouth diameter 0.7 m, mesh aperture 0.315 mm) at 50 stations.

Advanced-stage larvae and early juveniles of chub and Japanese Spanish mackerels were then collected in June and July, 1995 and 1996 from catches by a boat seine fishery, which operates primarily to fish Japanese anchovy *Engraulis japonicus* larvae and juveniles in the southern part of the survey area.

In cruises SO and SH, water temperature profiles were measured with STD. The volumes of seawater filtered by the nets were measured by a flowmeter mounted on the mouths of the nets and the ichthyoplankton catch from the horizontal and oblique hauls were converted to catch per 1000/m³ and 100/m², respectively. Ichthyoplankton samples were preserved in 10% formalin and a subsample of chub and Japanese Spanish mackerel larvae was preserved in 90% ethanol within 24 hours after 10% formalin fixation for otolith analysis. The standard lengths (SL) and upper jaw lengths (UJL) of 160 chub and 130 Japanese Spanish mackerel larvae were measured and mouth diameters (MD) were calculated by the equation, $MD = UJL^{0.5}$ according to Shirota (1970).

All of the samplings during cruises SO and SH and the boat seine fishery were conducted in the daytime (8:00 a.m. to 5:00 p.m.). A total of 420 chub and 479 Japanese Spanish mackerel larvae were analyzed for stomach contents.

Growth in the early life stages of chub and Japanese Spanish mackerel larvae were estimated from otolith increments according to validations for each species. Daily otolith rings begin to form at hatching in Japanese Spanish mackerel (Shoji *et al.*, 1999) and at yolk exhaustion in chub mackerel (Brothers *et al.*, 1983). Since chub mackerel larvae initiate exogenous feeding at 48 hours after hatching under 19°C (Watanabe, 1970), otolith ages were corrected by adding two days to the total counts. A total of 80 chub and 105 Japanese Spanish mackerel larvae and early juveniles collected during the cruises and the boat seine fishery sampling was examined for growth analysis. Right-side sagittal otoliths of larvae were removed under a dissecting microscope and otolith increments were counted under a compound microscope with a video monitor.

Separation of larval chub mackerel *Scomber japonicus* from its congener, spotted mackerel *Scomber australasicus* is difficult (Ozawa, 1988). The difference in pigmentation of larvae between the two species may not always be definitive and the early larvae we collected in the Seto Inland Sea might include both *Scomber* species. The spotted mackerel, however, spawn in more oceanic waters of southwestern Japan (Tanoue, 1966). Therefore, in this study, we considered all of the *Scomber* larvae we collected during the cruises to be chub mackerel *Scomber japonicus* that originated in the Seto Inland Sea.

Results

Occurrence and Distribution of Larvae

In cruise SO, 949 chub and 248 Japanese Spanish mackerel larvae were collected. Seasonal variations in density (1000/m³) of the larvae in 1995 and 1996 are shown in (Fig. 3). Both species were abundant from late May to early June, when the mean surface water temperature in late May was 18.0°C in 1995 and 18.3°C in 1996, and decreased after early June when the temperature averaged 18.9°C and 19.1°C, respectively. The seasonal occurrence of chub mackerel larvae was similar to that of Japanese Spanish mackerel larvae with a 10-day shift separating peak occurrence of the two species.

In cruise SH, 791 chub (2.3-10.4 mm SL) and 118 Japanese Spanish (3.6-10.8 mm SL) mackerel larvae were collected. On 27-30 May, which almost corresponds with the peak abundance of the two mackerels, the densities of chub mackerel larvae was higher at the central, southern and eastern stations (Fig. 4). Japanese Spanish mackerel larvae showed almost the same pattern of horizontal distribution as that of chub mackerel larvae, being abundant in the central and southern stations. On 18-21 June the two species were collected mainly at the central and southern stations, but less abundantly.

Figure 3. Seasonal variation of mean surface water temperature (WT) and mean density (number 1000/m³) of chub mackerel (CM) and Japanese Spanish mackerel (JSM) larvae obtained from the horizontal hauls (cruise SO) in the Hiuchi-nada in 1995 and 1996. E, M, and L indicate early, middle, and last 10 day periods of a month, respectively.

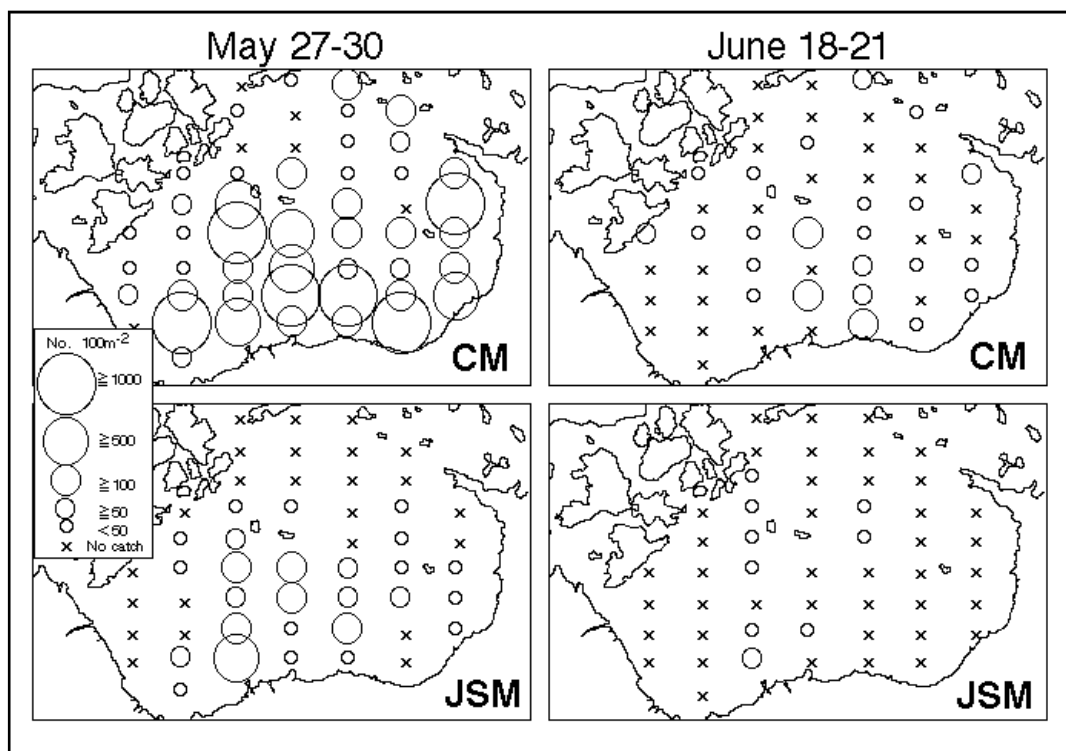
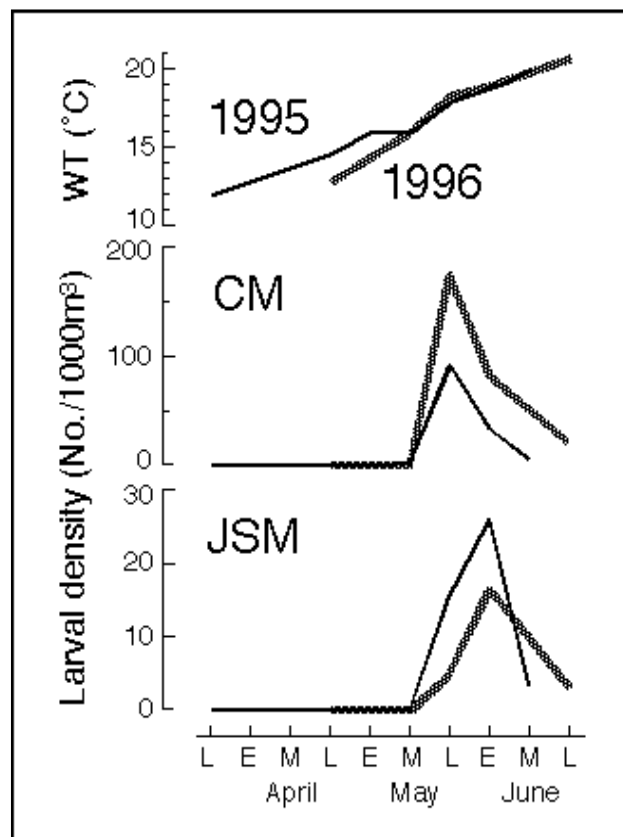


Figure 4. Distribution of chub mackerel (top: CM) and Japanese Spanish mackerel (bottom: JSM) larvae obtained from the oblique hauls (cruise SH) in the Hiuchi-nada on 27-30 May and 18-21 June in 1996.

Gut Contents

Analysis of gut contents revealed distinctive food habits between the two mackerel larvae (Table 1). Appendicularia, Copepoda and fish larvae were dominant taxa in the guts of chub mackerel larvae, occupying 34.0%, 30.8%, and 23.8% in number, respectively. Other invertebrate plankton taxa, such as invertebrate egg, Cladocera, Mysidacea and Decapoda occupied 0.5% to 3.2%. On the other hand, Japanese Spanish mackerel larvae fed almost exclusively on fish larvae despite the low numbers of invertebrate plankton observed. The dominant fish taxa eaten by chub and Japanese Spanish mackerel were Clupeiformes, which occupied 76.3% and 93.7%, respectively, of the identified fish in their stomachs.

Table 1. Feeding incidence and composition of stomach contents in terms of number of food items of chub mackerel (C) and Japanese Spanish mackerel (JSM) larvae.

	CM		JSM	
Size range (SL mm)	2.3-17.2		3.7-18.5	
No. of fish examined	420		479	
No. of fish feeding	358		411	
Guts with food (%)	85.2		85.8	
Contents	N	%	N	%
Invertebrate egg	14	2.1	1	0.2
Cladocera	3	0.5		
Copepoda	202	30.8	4	0.9
Mysidacea	21	3.2		
Decapoda	3	0.5		
Appendicularia	223	34.0		
Fish larva	156	23.8	386	90.8
Unidentified	34	5.2	34	8.0

The percentage occurrence of guts containing fish larvae is shown by size range in the two mackerel larvae (Fig. 5). None were found in the guts of chub mackerel larvae less than 5 mm SL. This percentage increased with chub mackerel larvae growth. Japanese Spanish mackerel larvae exhibited almost complete piscivory regardless of the larval size.

Mouth Size

Development of a large mouth, which may improve feeding efficiency, seems to affect the timing of the onset of piscivory in marine fish larvae. A previous study on the relationship between mouth size and prey size during the early life stages of chub mackerel revealed that the percentage of feeding success decreased as relative prey size (ratio of prey width to mouth width) increased (Hunter and Kimbrell, 1980). For piscivorous larval fish, mouth gape is considered an important factor in capturing piscine prey, which have advanced swimming

ability, compared to invertebrate plankton prey (Hunter, 1981). Mouth diameter, calculated using UJL, of the two mackerels larvae increased as the larval growth progressed (Fig.

6). Mouth diameter of Japanese Spanish mackerel larvae in the first feeding stage was about 1 mm, twice that of chub mackerel larvae. The relationship between standard length (L , mm) and mouth diameter (D , mm) was expressed by the following equation:

$$\text{chub mackerel: } D = 0.218 \cdot L - 0.241 \quad (n=160, r^2=0.97)$$

$$\text{Japanese Spanish mackerel: } D = 0.487 \cdot L - 1.431 \quad (n=130, r^2=0.92)$$

Figure 6. Relationship between mouth diameter (D , mm) and standard length (L , mm) of chub mackerel (CM) and Japanese Spanish mackerel (JSM) larvae.

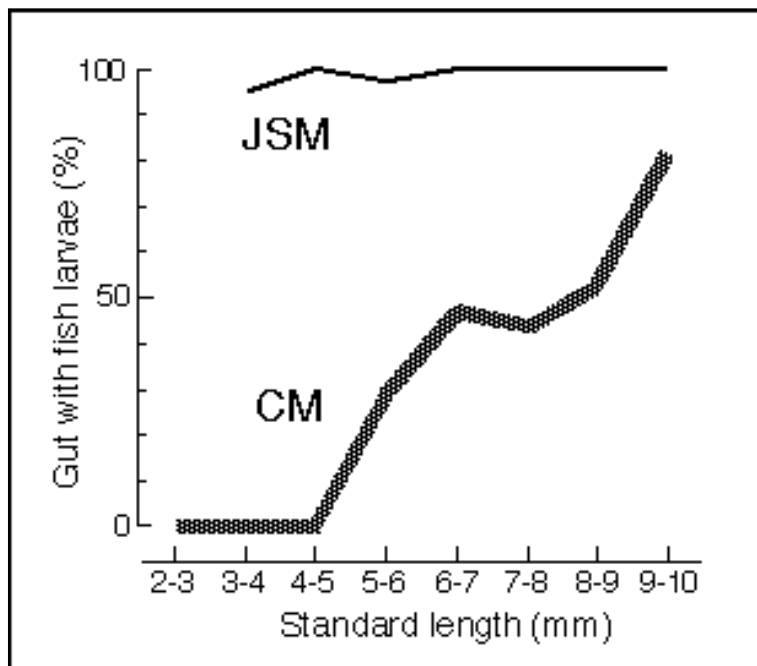


Figure 5. Percentage of chub mackerel (CM) and Japanese Spanish mackerel (JSM) larval guts with fish larvae. Each 1 mm size class includes more than 20 observations

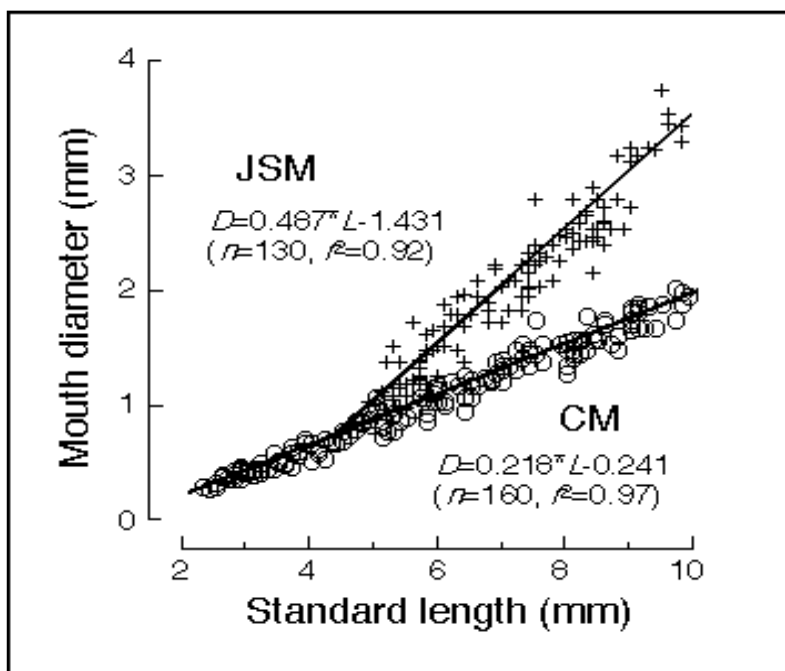
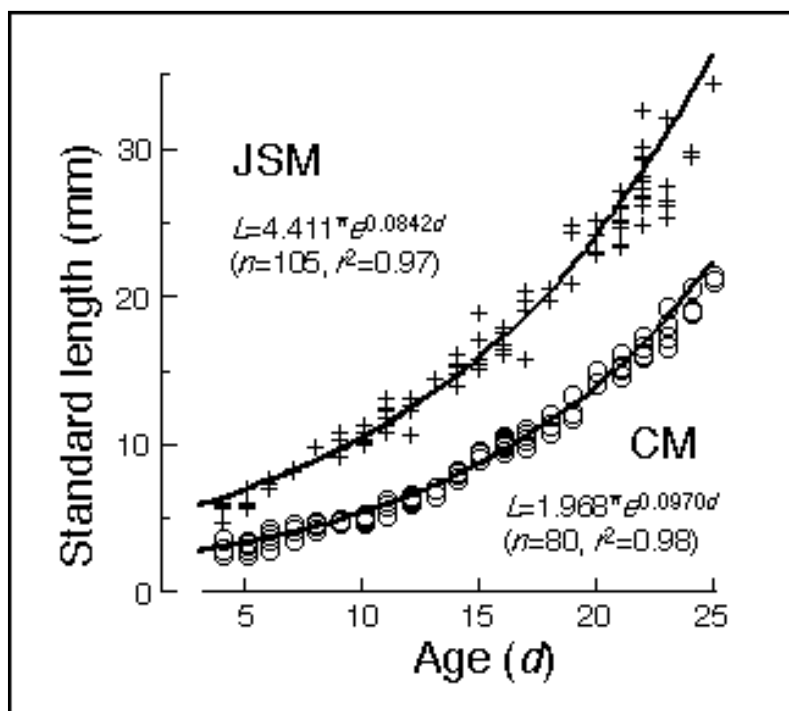


Figure 7. Relationship between standard length (L , mm) and estimated age in days (d) of chub mackerel (CM) and Japanese Spanish mackerel (JSM) larvae and early juveniles.

Growth

The relationship between standard length (L , mm) and age (d , days) during the larval and early juvenile stages was estimated from the otolith increments (Fig. 7) and expressed by the following exponential equations:



chub mackerel:	$L = 1.968 * e^{0.0970d} (n=80, r^2=0.98)$
Japanese Spanish mackerel:	$L = 4.411 * e^{0.0842d} (n=105, r^2=0.97)$

The two species had similar specific growth rates, from 8 to 10 % of standard length per day. The predicted absolute growth rate after first feeding varied between developmental stages and species (Table 2). Timing of first feeding of chub and Japanese Spanish mackerel larvae were considered as 2 and 5 days after hatching, respectively (Watanabe 1970; Shoji *et al.* 2001). The absolute growth rate of Japanese Spanish mackerel increased from approximately 0.7 mm/day in the post-first-feeding stage to approximately 1.5 mm/day in the early juvenile stage.

Table 2. Predicted absolute growth rates (mm/day) as a function of age from first feeding of chub mackerel (CM) and Japanese Spanish mackerel (JSM) larvae and juveniles.

Age (day)	CM	JSM
5	0.298	0.704
10	0.391	0.888
15	0.523	1.136
20	0.712	1.474

Discussion

Chub and Japanese Spanish mackerel larvae appear to have similar patterns of temporal and spatial distribution in the central Seto Inland Sea. They showed a similar pattern of seasonal occurrence from May to June in 1995 and 1996 (Fig. 3). In both species, seasonal peaks in larval densities were observed in late May to early June, suggesting a short spawning period. Larval distribution patterns were also similar. In late May 1996, during the seasonal peak of occurrence in both, they were most abundant at stations in the central and southern areas of the Hiuchi-nada (Fig. 4). The timing of spawning migrations into the Inland Sea and the seasonal peak of larval abundance of chub and Japanese Spanish mackerels were well matched with the seasonal peak of ichthyoplankton prey abundance (Mito, 1964).

In the Seto Inland Sea, chub mackerel larvae initially fed on invertebrate plankton, primarily Appendicularia and Copepoda (Fig. 5, Table 1). These animals were also dominant prey of the chub mackerel in the southwestern waters of Japan (Yokota *et al.*, 1961) and the southeastern Pacific (Lipskaya, 1982) waters of Japan. Fish appeared in the diet of chub mackerel larvae at the 5-6 mm SL size class and became more common as larval growth proceeded (Fig. 5). At 5-6 mm SL, the mouth diameter of chub mackerel larvae reached that of Japanese Spanish mackerel larvae at the first feeding (Fig. 6). Jaw and pharyngeal teeth (Kohno *et al.*, 1984) and digestive structures (Tanaka *et al.*, 1996) begin to develop between 5.0 to 7.0 mm SL in chub mackerel. These morphological developments are considered to be associated with the onset of piscivory.

Compared to our observations in the Seto Inland Sea, the onset of piscivory of chub mackerel larvae seems to be later in oceanic waters, such as southwestern Japan (Yokota *et al.*, 1961), where chub mackerel larvae smaller than 8 mm fed only on invertebrate plankters. These results suggest that chub mackerel larvae can use flexibly two feeding tactics, planktivory and piscivory, depending on food availability in the water. Spawning migrations of many fishes into the Inland Sea result in rapid increase in ichthyoplankton density from spring to summer (Mito, 1964; Shoji *et al.*, 1999). Higher food availability in the Seto Inland Sea than in the oceanic waters may allow the earlier onset of piscivory of the chub mackerel larvae observed in this study.

Piscivory was observed in Japanese Spanish mackerel larvae from the first feeding stage. The intensity of piscivory did not fluctuate with larval size (Fig. 5). Other fish larvae contributed to the majority of the stomach contents, while invertebrate plankters were seldom observed (Table 1).

Scombrid larvae generally have large eyes and a mouth and exhibit an early shift from planktivory to piscivory relative to other marine fish larvae (Hunter 1981). Some tuna larvae, such as bluefin tuna *Thunnus thynnus* and skipjack tuna *Katsuwonus pelamis*, have large eyes and mouth gapes (Shirota, 1978; Uotani *et al.*, 1990) and exhibit piscivory in their early life stages (Nishikawa, 1975; Uotani *et al.*, 1981; Young and Davis, 1990). In these species, however, piscivory appears to develop at a more advanced stage. We speculate that there are other factors affecting the onset of piscivory in scombrid larvae. First, size at initial feeding should be important because larger size enables capture of relatively large prey. Japanese Spanish mackerel larvae hatch from large eggs (1.35 to 1.85 mm in diameter) and exhaust their yolks at 6.0 mm SL (Xue-shen *et al.*, 1966), while egg size (less than 1.2 mm; Mito, 1961) and larval size at yolk exhaustion (less than 4 mm; Yabe *et al.*, 1966; Ueyanagi *et al.*, 1974) are smaller in these tunas. Secondly, development of the digestive system also seems to be related to the early onset of piscivory. Tanaka *et al.* (1996) showed precocious development of an adult-type digestive system with a functional stomach and pyloric caeca of laboratory-reared Japanese Spanish mackerel larvae. Finally, an instinctive factor seems to be important, where Japanese Spanish mackerel larvae began to cannibalize when supplied with

only invertebrate plankton prey under rearing conditions (Fukunaga *et al.*, 1982; Shoji and Tanaka, 2001).

Our study supports the previous reports of higher growth rates during early life stages of members of the genus *Scomberomorus* than that of *Scomber* species. The absolute growth rate of the chub mackerel obtained from this study (0.712 mm/day, up to 20 days after first feeding, Table 2) was similar to that of Atlantic mackerel from the middle Atlantic Bight (Kendall and Gordon, 1981). In laboratory experiments, Hunter and Kimbrell (1980) observed that rapid increase in prey size was required to support rapid growth of chub mackerel larvae. In this study, absolute growth of sea-caught chub mackerel increased from 0.298 mm/day (post-first-feeding stage) to 0.712 mm/day (later larval and early juvenile stages). The increase in growth rate of chub mackerel observed in this study may result from the feeding shift to piscivory indicated by the analysis on the wild larvae (Fig. 5).

Higher growth rates were observed in king mackerel *Scomberomorus cavalla* (1.31 mm/day) and Spanish mackerel *Scomberomorus maculatus* (0.82 mm/day) larvae from the Gulf of Mexico and U. S. South Atlantic Bight (DeVries *et al.*, 1990). These rates were close to the absolute growth rate of the Japanese Spanish mackerel larvae and early juveniles up to 10 and 15 days after first feeding (0.888 and 1.136 mm/day, respectively, Table 2). The higher growth rates observed in *Scomberomorus* larvae are probably related to the specialized food habits at early onset of piscivory (DeVries *et al.*, 1990; Finucane *et al.*, 1990; Shoji *et al.*, 1997). Compared with the chub mackerel's relatively flexible feeding habits, Japanese Spanish mackerel larvae seem to have evolved a more specialized strategy of complete piscivory from the first feeding stage. Growth and survival of Japanese Spanish mackerel larvae may be highly dependent on piscine prey abundance relative to chub mackerel and other planktivorous larvae.

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